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HERBIVORY AND THE ENDANGERED ROBUST SPINEFLOWER (*CHORIZANTHE ROBUSTA* VAR. *ROBUSTA*)

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ABSTRACT

Insect herbivory has been shown to have substantial impacts on plant growth and reproduction in many systems. However, the effect of insect herbivores on rare and endangered plants has not been widely studied, even though natural limitations on growth and reproduction, in combination with anthropogenic changes in habitat quality and quantity, likely contribute to population decline. In the current study, an insect exclusion experiment was used to assess the effects of insect herbivory on a federally listed endangered annual plant: *Chorizanthe robusta* var. *robusta* (Polygonaceae). The primary insect herbivore was a microlepidopteran larva, an undescribed species of *Aroga* (Gelechiidae). Excluding *Aroga* larvae led to a 30% increase in seed output compared to water control. No change in plant survivorship or seed/flower ratios was found with insect exclusion. Control plants given supplemental water had increased seed production, but only in the absence of *Aroga* infestation, an indication that infested plants could not fully exploit additional resources. These results show that rare annuals are potential host plants for insect herbivores, and herbivory is an important factor to consider when evaluating endangered plant populations.

Key Words: insect exclusion, rare plants, sand dunes, *Aroga*, Gelechiidae.

Endangered plants characteristically have populations that are limited in size and extent, often due to habitat loss caused by human activities. In coastal areas of California, urban development and agriculture have reduced natural areas considerably. Under these conditions, any additional factor that reduces survivorship or reproduction of a rare species can contribute to the possibility of extinction. Numerous studies have shown that insect herbivores reduce survivorship, growth, and reproductive output of plants (Rausher and Feeny 1980; Louda 1982, 1984; Crawley 1983, 1989). In many cases plant fecundity is more dramatically limited by herbivory than is survivorship, and an increase in seed number is often found when herbivores are excluded, even when herbivory is at very low levels (Crawley 1983; Kinsman and Platt 1984; Brown et al. 1987; Root 1996; Wise and Sacchi 1996; Mauricio 1998; Parmesan 2000; Maron 2001). Leaf and flower damage from herbivory can also indirectly affect seed production by decreasing pollination rates (Mothershead and Marquis 2000). Although these effects of herbivory on plant performance are well documented, the question of how herbivores affect plant populations is still widely debated (Crawley 1983, 1989; Carson and Root 2000). Some studies have shown that a reduction in seed by herbivores is likely to lead to a reduction in plant abundance (Louda 1982; Louda and Potvin 1995; Wise and Sacchi 1996; Fagan and Bishop 2000; Maron 2001), but density-dependent mortality or a shortage of germination sites can negate this effect (Crawley and Gillman 1989; Maron and Gardner 2000). However, research has shown that small populations of endangered plants can be restricted by low seed production (Pavlik et al. 1993; Bevill et al. 1999) so we can not discount herbivory when evaluating rare plants. Plants can be rare for a variety of reasons (see Rabinowitz 1981), but the end result is often small population size. Projections of population growth or decline are impossible to make without first identifying the factors which reduce plant survivorship and reproduction, and discerning the vulnerable life stages (Pavlik et al. 1993; Schemske et al. 1994).

Excluding herbivores from a subset of plants and comparing plant performance is the best way to assess the effects of herbivory in wild plant populations (Crawley 1989), and this was the method used for this study. Plant competition and availability of resources must also be considered, as these factors can work in concert with herbivory to affect plant growth and reproduction. For example, limited resources can increase the effect of herbivory on individual plants by restricting growth (Louda 1984; Louda et al. 1990), but some studies have shown that even when resources are plentiful, plants cannot overcome the effects of herbivory, especially annual plants (Pavlik et al. 1993; Wise and Sacchi 1996).

The current study seeks to determine if insect herbivory reduces survivorship, growth, and seed output of *Chorizanthe robusta* var. *robusta* C. Parry (Polygonaceae), a federally listed endangered plant. Mammal herbivores are often important in sand dune habitats (Palmisano and Fox 1997); however, no mammal herbivory was seen in preliminary

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studies on *C. robusta* at two sites over two years (personal observation), and Swank and Oechel (1991) noted that rabbits rarely grazed *Chorizanthe fimbriata* and *C. polygonides* in their study in chaparral. Consequently, only insects were excluded in this study.

Herbivore density can vary between small and large patches of host plants (Bach 1988). Because herbivore density patterns are an important factor in predictive models, the relationship between clearing size and herbivory was also investigated.

Methods

Plant Species

Chorizanthe robusta var. *robusta* is an annual spineflower that inhabits sandy soil sites in Santa Cruz County, CA. Plants are low-growing and extremely variable in size, forming a single upright stem or having multiple branches. *Chorizanthe robusta* germinates in the winter and flowers from April through June or July. Each plant produces multiple small flowers and each flower can produce one seed. Seeds are dispersed in involucres with hooked awns that can attach to passing animals. *Chorizanthe* colonizes along trails and in clearings over the landscape. At the study site, some of these clearings are very large with thousands of plants and others are small with only a few individuals encircled by shrubs. This plant is federally listed as endangered and is known from seven populations, some less than 100 plants (USFWS 2000). The genus *Chorizanthe* is taxonomically challenging, with many closely related species, subspecies, and varieties in California (Ertter 1996). There are taxonomic uncertainties about *C. robusta* at the study site due to the proximity of a closely related species *Chorizanthe pungens* (Benth). *Chorizanthe pungens* is thought to grow primarily on the fore dunes and *Chorizanthe robusta* primarily on the rear dunes; however, no published studies have quantified the genetic structure of the species complex. The plants chosen for this study were on the rear dunes and morphologically similar to *Chorizanthe robusta* var. *robusta* at other sites.

Insect Herbivore

Although this study examined the effect of excluding all chewing insects, the primary insect herbivore on *C. robusta* were larvae of an undescribed moth species in the genus *Aroga* (Gelechiidae) (J. Powell personal communication). These larvae create silken shelters covered with sand and litter, attached to the base of *C. robusta* plants. They feed on leaves and are active from March through June. Pupation occurs in shelters on or near the soil surface. Adult specimens were collected in the field in early August.

Study Site

Sunset State Beach was selected as the location for this study because the largest known population of *C. robusta* (many thousands of plants) occurs over a wide area on the rear dunes. Sunset State Beach is located in central California just west of the town of Watsonville (36°52.89′N, 121°49.69′W). The study site was within a 300 square meter area on the top of a rear dune. These rear dunes are stable and dominated by coastal scrub species such as *Ericameria ericoides* (Less.) Jepson (Asteraceae). The habitat is a mosaic of various sized openings between shrubs with sand, moss, grasses, bracken fern, and forbs. *Chorizanthe robusta* grows in dense patches in these openings. Much of the study site is colonized by *Syntrichia princeps* (De Not.) Mitt [*Tortula princeps*], a low growing moss that forms mats in which *C. robusta* and other forbs grow.

The central coast of California has a moderate mediterranean climate. During the study period (October 2000–April 2001), the average monthly temperature of 12°C was normal for this period. An average monthly rainfall of 2.4 inches was 79% of normal for this period. The last measurable rainfall for the season was on or about April 18, 2001 (U.S. Dept. of Commerce 2002).

Experimental Design

An insect exclusion experiment with three treatments was performed to assess the effects of herbivory on plant survivorship, plant size, and seed output. In one set of plants insects were excluded by using an insecticide spray, Carbaryl (1-naphthol *N*-methylcarbamate), a ready-mixed aqueous solution of a wide-spectrum carbamate insecticide, brand name Sevin (Rhone-Poulenc). Carbaryl kills chewing insects for three to ten days, and has a half life of seven days in aerobic soil (PMEP 1993). Prior studies on this insecticide indicate that its effects on plant growth are minimal (Jones et al. 1986; Gibson et al. 1990). Because spraying of water may influence growth and seed production, two controls were included to assess the effect of insect exclusion with an insecticide independent of spraying. The first control included plants that were sprayed in the same manner as the insecticide but with water only. For the second control, the plants were not sprayed. Every seven to ten days from March 17 to May 14, 2001, until plants were in flower, insecticide and water spray treatments were applied in the morning when winds were calm and temperatures low.

A randomized block design was used to minimize effects from microhabitat variation. Fifty blocks, each with three plants of similar size growing near each other, were randomly selected. Each plant in the block was assigned a different treatment, and the order of assignment was randomized.

Four types of measurements were made. Plants were inspected weekly for the duration of the study

TABLE 1. RANDOMIZED COMPLETE BLOCK ANCOVA FOR TESTING THE EFFECT OF EXCLUDING INSECT HERBIVORES ON NUMBER OF SEEDS PER PLANT. Independent variable was Treatment with three levels, Insect exclusion (IE), Water spray control (W), and Non-spray control (N). Dependent variable was number of seeds per plant (ln transformed). Blocks were randomly selected groups of three plants. Covariate was final plant density.

Source	SS	df	MS	F	P
Treatment	9.401	2	4.700	3.657	0.038
IE vs. W	7.305	1	7.305	5.683	0.023
W vs. N	0.004	1	0.004	0.003	0.956
Block	31.478	16	1.967	1.530	0.151
Final Plant Density	8.983	1	8.983	6.989	0.013
Error	39.848	31	1.285		

to monitor survivorship and determine whether they had been infested with *Aroga*. Local plant density was measured at the beginning and end of the experiment by positioning each study plant in the center of a 10-cm square, and counting all plants within the square. In addition, the size of each clearing (with study plants) was measured. After seed set, plants were collected to measure plant size, number of seeds, and number of flowers. Because *Chorizanthe robusta* has small sparsely distributed leaves along with highly variable stems and branches, the sum of the length of all branches plus the length of the stem was used as a measure of plant size. For each plant, seed/flower ratios were also computed.

Randomized Complete Block Analysis of Covariance (Zar 1996) was used to assess the effect of excluding insect herbivores on plant size (total length of branches plus stem), number of seeds, and seed/flower ratios. For all analyses, the independent variable was Treatment with three levels, insect exclusion by application of insecticide, water spray control, and the non-spray control. Plant size and number of seeds were transformed for analysis as ln(x) because variances of the untransformed variables were not homogeneous among treatments. Blocks in the analyses were the randomly selected groups of plants. To insure that the treatments within a block really represented cases where herbivores were excluded or not, only those blocks in which *Aroga* occurred were considered for analyses. Blocks in which one or more plants died or in which grazing by rabbits occurred during the experiment were also excluded from analyses. For each dependent variable, two a priori comparisons were performed to compare treatments. To assess whether the application of insecticide affected plant size or number of seeds, the insect exclusion treatment was compared to the water spray control. Because final plant density was correlated with plant size ($r = -0.493$) and number of seeds ($r = 0.484$), final plant density was included in the analyses as a covariate. To determine if there was a difference in the effect of watering between infested and non-infested plants, all watered plants were analyzed using ANCOVA with Infested as the independent variable, and seed number and plant size as dependent variables. Final plant density was included as a covariate.

To evaluate the effect of plant patch size on sources of herbivory, 145 plants in patches of varying sizes were examined throughout the study period. Patches were identified as groups of plants surrounded by shrubs. The area of each patch was measured in square meters (length × width). Patches were classified by area into three groups: Small: 0–3.00 m^2, Medium: 3.01–7.00 m^2, and Large: 7.01–10.00 m^2. Evidence of rabbit grazing and infestation by *Aroga* was recorded for each patch. A 2×2 Test of Independence (Zar 1996) was used to determine if there was a relationship between the presence or absence of rabbit grazing and patch size. The same type of test was used to determine if the presence or absence of *Aroga* larvae was independent of patch size.

RESULTS

Plant mortality was extremely low during this study. Only two (out of 150) study plants died and both were due to gopher activity. However, rabbits (*Sylvilagus bachmani* Grinnell and Storer) removed mature seed heads late in the season from 11% of study plants, effectively eliminating their reproductive potential.

The RCB ANCOVA showed that seed number increased when insects were excluded (Table 1). The first a priori comparison showed that mean number of seeds per plant (ln transformed) was greater ($P < 0.023$) in the insect exclusion treatment as compared to the water spray control (Fig. 1). The second a priori comparison showed that mean number of seeds per plant did not differ ($P = 0.956$) between the water spray control and the non-spray control (Fig. 1). The block effect was not significant ($P = 0.151$) indicating that a block design was not necessary. However, final plant density was a significant covariate ($P = 0.013$). ANCOVA for seed/flower ratios showed no significant difference among treatments ($P = 0.211$).

The results for plant size were similar to the results for number of seeds (Table 2). The RCB ANCOVA showed that plant size increased when insects were excluded. The first a priori comparison

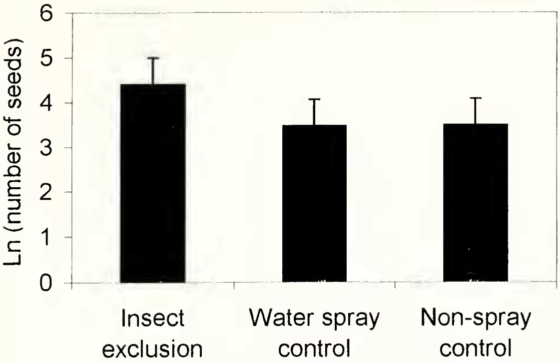

FIG. 1. Mean number of seeds per plant (ln transformed) for the three treatments, Insect exclusion, Water spray control, and Non-spray control, adjusted for final plant density. Error bars are 95% confidence limits.

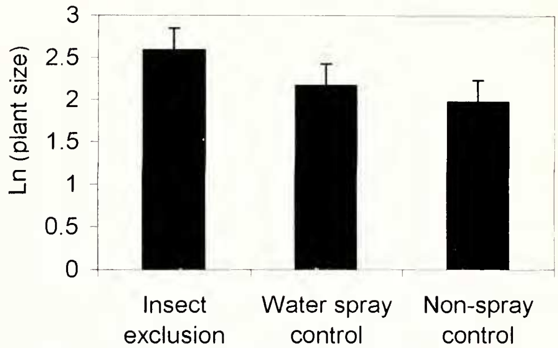

FIG. 2. Mean plant size per plant (cm) (ln transformed) for the three treatments, Insect exclusion, Water spray control, and Non-spray control, adjusted for final plant density. Error bars are 95% confidence limits.

showed that mean length of branches plus stem per plant (ln transformed) was greater ($P < 0.026$) in the insect exclusion treatment as compared to the water spray control (Fig. 2). The second a priori comparison showed that mean length of branches plus stem per plant did not differ ($P = 0.273$) between the water spray control and the non-spray control. The block effect was barely significant ($P = 0.050$) indicating that a block design was desirable for experiments in which plant size was the measured variable. As with the analysis for number of seeds, final plant density was a significant covariate ($P = 0.040$).

The effect of watering differed for infested vs. non-infested plants. Average seed number was significantly higher for non-infested plants ($P < 0.02$) and final density was an important covariate (Table 3, Fig. 3).

Both rabbit grazing and presence of *Aroga* larvae appeared to be related to plant patch size. The results of the 2×2 Test of Independence showed that plant patch size was related to the presence or absence of rabbits (Log-likelihood ratio = 23.508, df = 2, $P < 0.001$); rabbit grazing tended to occur more often in the smallest plots (Fig. 4). Patch size was also related to the presence or absence of *Aroga* larvae (Log-likelihood ratio = 9.415, df = 2, $P < 0.010$). During this study, 34% of plants not sprayed with insecticide had signs of *Aroga* infestation and *Aroga* larvae tended to appear in larger patches of plants (Fig. 5).

DISCUSSION

The results of this study indicate that insect herbivores significantly reduced both size and lifetime seed production of these annual plants, factors that could have far reaching effects on a small population (Table 1). Since seed/flower ratios did not differ for insecticide treated plants, insects reduced seed production by reducing plant size (or resource allocation) rather than pollination rates. Plant size has often been found to be correlated with seed output (Rausher and Feeny 1980; Wolfe 1983; Brown et al. 1987; Stöcklin and Favre 1994). Potential growth effects from insecticide use must also be considered. In the absence of herbivory, insecticide treated plants were no larger on average (16.8 cm) than plants sprayed with only water (17.2 cm). Because other studies have shown that Carbaryl has a negative or minimal effect on plant growth (Jones et al. 1986; Gibson et al. 1990) it is unlikely that Carbaryl induced plant growth in this study.

Additional water increased seed output, but only in plants without *Aroga* infestation (Fig. 3). Other studies have also found that abundant or supplemental water did not produce an increase in seed

TABLE 2. RANDOMIZED COMPLETE BLOCK ANCOVA FOR TESTING THE EFFECT OF EXCLUDING INSECT HERBIVORES ON PLANT SIZE. Independent variable was Treatment with three levels, Insect exclusion (IE), Water spray control (W) and Non-spray control (N). Dependent variable was total branch length plus stem per plant (ln transformed). Blocks were randomly selected groups of three plants. Covariate was final plant density.

Source	SS	df	MS	F	P
Treatment	2.237	2	1.619	6.091	0.006
IE vs. W	1.449	1	1.449	5.454	0.026
W vs. N	0.331	1	0.331	1.245	0.273
Block	8.424	16	0.527	1.981	0.050
Final Plant Density	1.223	1	1.223	4.602	0.040
Error	8.239	31	0.266		

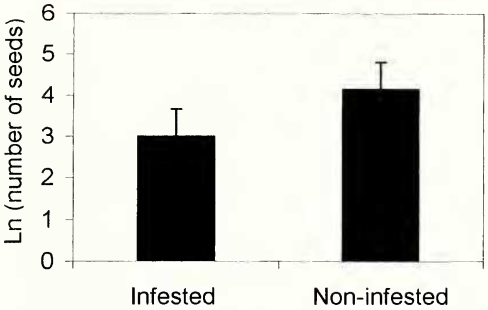

FIG. 3. Mean number of seeds per plant (ln transformed) for infested vs. non-infested water sprayed plants, adjusted for final plant density. Error bars are 95% confidence limits.

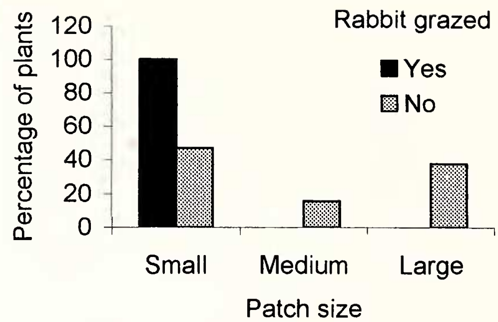

FIG. 4. Plant patch size (small = 0–3.00 m^2, medium = 3.01–7.00 m^2, large = 7.01–10.00 m^2) vs. presence or absence of rabbit grazing.

output in plants subject to herbivory (Swank and Oechel 1991; Pavlik et al. 1993; Wise and Sacchi 1996). Because *Aroga* larvae remove leaves, they compromise the plant's ability to garner resources (Louda 1984; Louda et al. 1990). This potential interaction between herbivory and resource uptake and allocation is an important factor to consider in rare plant management. If models are used to predict plant population growth, it may be necessary to include potential differences in resource utilization by the proportion of the population subject to insect herbivory.

Decreased seed production is a potential threat to the long term viability of this plant population only if it is seed limited (Louda 1982; Crawley 1983, 1989). A reduced seed supply may not affect a population with a shortage of "safe sites" for germination (Crawley and Gillman 1989). However, "safe site" availability can be difficult to determine because it can vary over years and over the landscape (Maron and Gardner 2000). In sand dune habitats it is likely that the availability of germination sites fluctuate yearly due to shrub growth and small scale disturbances. Research has shown that annual plants in sand dune environments often show evidence of seed limitation (Turnbull et al. 2000). Seed reduction can also have a greater impact on a plant species, such as *C. robusta,* that has metapopulation dynamics (Bevill et al. 1999), defined as sub-populations connected by dispersal (Eriksson 1996). Ecological factors such as these, combined with a loss of habitat due to human activities, may intensify the effects of herbivory and cause proportionally greater threats to rare and endangered plant populations.

There was some evidence that herbivores were selecting plants based on an environmental condition: clearing size. Larvae were more often found in the largest clearings, and rabbit grazing was more prevalent in small clearings and at the edges where shrubs were dense (Figs. 4 and 5). Herbivore density patterns will be important to include in predictive models, but they may also have evolutionary consequences. According to John Thompson (personal communication), selection based on an environmental variable can increase the potential for genetic polymorphisms. In addition, the discovery of a possibly specialist herbivore presents future research opportunities that may help shed light on *Chorizanthe* taxonomy. Evolutionary relationships between species can evolve over small time scales, even decades, and changes in the distribution of metapopulations are one of the "normal processes of evolution" (Thompson 1998). More research is needed to determine if this moth species is a specialist on *Chorizanthe.* Although it is unusual for an annual plant to have a specialist herbivore (Crawley 1983), most small moths are specialists and they can survive in small habitat patches (Powell 1999). In a study of the range size of host plants for a variety of insect herbivores in England, Hopkins et al. (2002) found that a number of "micro moths" were associated with rare plants. Microlepidoptera such as these are not well studied and 50% to 90% of species with small adults col-

TABLE 3. ANCOVA FOR TESTING THE EFFECT OF WATER ON SEED NUMBER. Independent variable was Infestation with two levels, Yes (Y) and No (N). Dependent variable was number of seeds per plant (ln transformed). Covariate was final plant density.

Source	SS	df	MS	F	P
Y vs. N	8.857	1	8.857	6.094	0.020
Final Plant Density	29.770	1	29.770	20.483	0.000
Error	39.241	27	1.453		

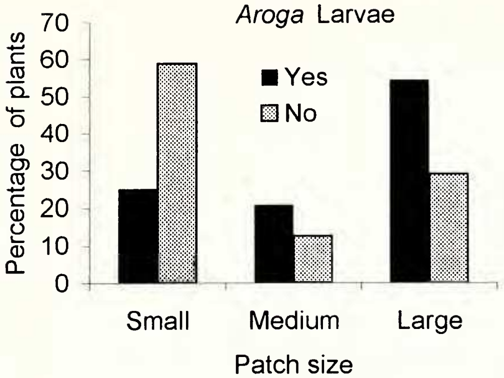

FIG. 5. Plant patch size (small = 0–3.00 m^2, medium = 3.01–7.00 m^2, large = 7.01–10.00 m^2) vs. presence or absence of *Aroga* larvae.

lected in California, remain undescribed (Powell 1999). This little known group is likely closely associated with our native flora. Rare plants are potential host plants for insects that are often cryptic and easily overlooked. These insects may be endangered themselves, illustrating how the loss of an annual plant species can decrease biodiversity at multiple scales. Understanding these important relationships will help us to better understand the ecology of rare plants and help shed light on causes of yearly fluctuation in wild plant populations.

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